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HEAD SIZE OF MALE AND FEMALE LIZARDS INCREASES WITH POPULATION DENSITY ACROSS ISLAND POPULATIONS IN THE BAHAMAS

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ABSTRACT.   In polygynous lizards, male–male competition is an important driver of morphologic and behavioral traits associated with intraspecific dominance. The extent to which females engage in aggressive behavior and thus contribute to competition-driven morphologic variation is not well studied. We used injury frequencies of brown anoles (*Anolis sagrei*) in 16 island populations to test the hypothesis that injury-inducing aggressive encounters increase with population density in both male and female lizards. We further asked whether intraspecific competition is a potential driver of phenotypic traits related to dominance by using population density as proxy for intraspecific competition. We found that the proportion of individuals with injuries was greater in populations with higher densities, suggesting that agonistic competitive interactions increase with population density. Size-adjusted head length of male and female lizards increased with population density, suggesting that larger heads might be advantageous when intraspecific competition is strong. We detected differences in morphology and injury frequency among islands for both males and females, which suggests that agonistic competitive interactions among females may be stronger than previously appreciated. Further research is needed to determine whether aggressive encounters involving females are restricted to intrasexual competition or whether they also involve males, and how morphologic traits of females are related to competitive dominance and reproductive success.

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INTRODUCTION

In many vertebrate species, males compete for mating opportunities and engage regularly in aggressive male–male interactions (Kokko and Rankin, 2006; Knell, 2009). In polygynous species, dominant males mate with the majority of females in their territories, whereas subordinate ones reproduce substantially less, if at all (Kokko and Rankin, 2006). Thus, the ability to obtain and defend territories disproportionally increases reproductive success for males in such species, and sexual selection is expected to shape the phenotypic traits associated with dominance and performance during aggressive male–male interactions.

In lizards, morphologic traits associated with dominance and performance in male–male competition are well characterized. Larger males hold larger territories in the wild (Lappin and Husak, 2005) and tend to "win" over smaller ones in staged encounters (Lailvaux et al., 2004; Jenssen et al., 2005). When equally sized males are matched, head size and bite force are key predictors of dominance (Gvozdík and Damme, 2003; Lailvaux et al., 2004; Perry et al., 2004). In most lizard species, body size is correlated with head size and bite force and thus is the primary trait linked to reproductive success of males (Herrel et al., 2001, 2007, 2010; Verwaijen et al., 2002; Wittorski et al., 2016; but see Lappin and Husak, 2005). Whereas the idea that sexual selection shapes body size, and head size has been supported empirically in several lizard species (Jenssen et al., 2000; Lailvaux et al., 2004; Perry et al., 2004; Calsbeek and Smith, 2007; Donihue et al., 2016;), most studies lack direct measures of aggressive behavior and its effects on individuals. Additionally, the extent to which aggressive behavior among females contrib-

utes to phenotypic evolution is not well studied, primarily because past studies have mostly focused on males.

Females are often described as less aggressive (Claessen et al., 2000) and less territorial (Schoener and Schoener, 1982; Nunez et al., 1997) than males, devoting more time to resource acquisition than to competition with conspecifics. In many lizard species, females have smaller body and head size and disproportionally weaker bite force than males, even when corrected for body size (Lappin et al., 2006; Wittorski et al., 2016). Such sexual dimorphism has led to the interpretation that intraspecific competition plays a minor role in shaping morphologic characters of female lizards (Lappin et al., 2006; Herrel et al., 2010; Wittorski et al., 2016). However, the few available studies that have included females suggest that aggressive behavior might be a relevant driver of morphologic characters in both sexes (Comendant et al., 2003; Calsbeek and Smith, 2007).

Injuries are a frequent consequence of intraspecific competition (Fig. 1) and can be used as a proxy for aggressive interactions (Gvozdik, 2000; Donihue et al., 2016). Biting

Figure 1. Two male brown anoles fighting near Staniel Cay in the Exumas, Bahamas (Photo by R. Pringle taken on May 5, 2015).

and jaw locking during agonistic encounters leave bite scars and can amputate body appendages such as claws, digits, limbs, and tails (Vervust et al., 2009; Brock et al., 2015; Donihue et al., 2016). Although limb-related injuries have been strongly linked with intraspecific aggression, tail amputations in species with caudal autotomy are more ambiguous (Schoener and Schoener, 1980; Gvozdik, 2000; Brock et al., 2015). The frequency of tail amputations can vary with species richness, predation regime, and the strength of intraspecific aggression (Cooper et al., 2004; Pafilis et al., 2009; Brock et al., 2015). Caudal autotomy is widely regarded as an adaptation for predator evasion, and tails are shed more easily (requiring lower bite force) in populations with predators compared with predator-free populations, making interpretation of this measure more difficult (Cooper et al., 2004; Pafilis et al., 2009; Brock et al., 2015). Accordingly, limb-related injuries may be a valuable indicator of the relative strength of intraspecific competition among populations.

In this study, we use brown anoles (*Anolis sagrei*) from 16 island populations in the Bahamas to test whether intraspecific competition is a potential driver of phenotypic traits in males and females. We use the frequency of injuries as a proxy for the frequency of aggressive intraspecific encounters. If intraspecific competition is higher in populations with higher densities, then we expect the proportion of injuries to increase with population density. Because larger body and head size enhance dominance and performance during male–male competition (Gvozdík and Damme, 2003; Lailvaux et al., 2004; Perry et al., 2004; Jenssen et al., 2005), we expect larger lizards with larger heads in higher density populations. We predict the same relationships for females: higher injury percentages and larger body and head size in populations with higher densities.
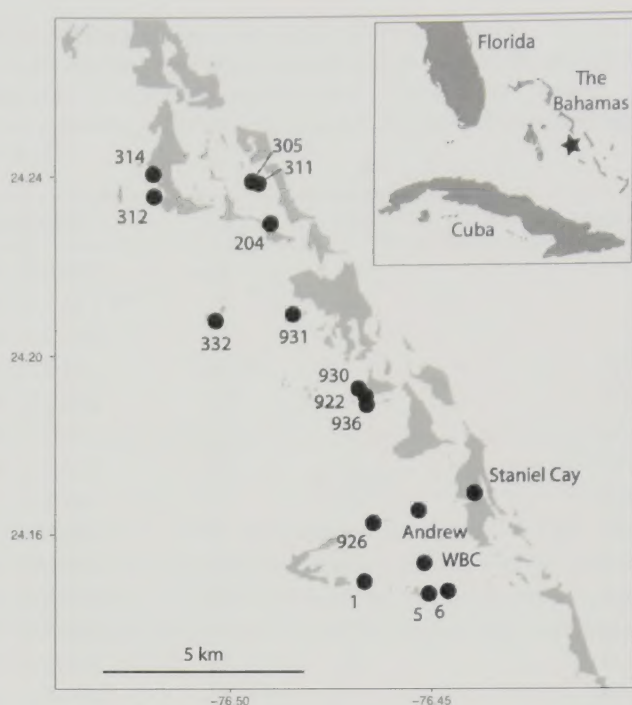

Figure 2. Map showing the location of the 16 islands in this study in relation to Staniel Cay in the Exumas, Bahamas.

MATERIAL AND METHODS

Sampling and morphologic measurements

Male and female brown anoles were collected in May 2011 on 16 small islands in the Bahamas near Staniel Cay in the Exumas (Fig. 2), where they were the only lizard species present ($N_{\text{female}} = 178$; $N_{\text{male}} = 244$; Table 1). Notably, these islands lacked widespread competitors (green anoles, *Anolis smaragdinus*) and predators (curly tailed lizards, *Leiocephalus carinatus*) of brown anoles that are present on some islands in the area. These species were subsequently introduced to subsets of these islands as part of an experiment (Pringle et al., 2019). We took X-ray images and digital scans of live lizards and scored injuries as the number of missing claws, digits, and limbs from the X-ray and scanner images. We measured body size (snout–vent length [SVL]), head length, and head width at its widest point from X-

TABLE 1. SAMPLE SIZES OF MALE AND FEMALE LIZARDS, ISLAND AREAS, POPULATION DENSITIES, AND INJURY PERCENTAGES FOR THE 16 ISLAND POPULATIONS OF BROWN ANOLES. N_F = NUMBER OF SAMPLED FEMALES, N_M = NUMBER OF SAMPLED MALES; ABUNDANCE = POPULATION ESTIMATE ± SD; AREA = VEGETATED AREA; DENSITY = POPULATION DENSITY (ABUNDANCE DIVIDED BY AREA); AND INJURY = NUMBER OF LIZARDS WITH AN INJURY DIVIDED BY THE TOTAL SAMPLED ON EACH ISLAND.

Island	N_F	N_M	Abundance	Area (m^2)	Density	Injury (%)
1	16	12	264.6 ± 46.2	1,429	0.19	36
5	16	15	120.1 ± 13.5	1,333	0.09	32
6	15	16	362.2 ± 58.8	1,851	0.18	32
204	7	10	64.0 ± 14.0	487	0.13	41
305	9	15	263.6 ± 66.7	603	0.31	50
311	7	14	445 ± 80.7	2,241	0.20	43
312	15	16	124.3 ± 14.5	640	0.19	26
314	17	13	146.1 ± 13.3	1,400	0.10	20
332	6	6	41.8 ± 5.8	1,450	0.04	17
922	4	18	202.8 ± 60.1	1,648	0.12	18
926	17	13	385.8 ± 69	3,320	0.11	3
930	12	16	309.5 ± 35.2	2,582	0.12	7
931	12	18	249.8 ± 27.3	1,070	0.23	17
936	7	23	423.6 ± 62.9	2,772	0.13	20
Andrew	8	19	195 ± 42.6	1,758	0.11	26
White Bay Cay	10	20	155.7 ± 19.1	1,575	0.10	37

ray images with the plug-in ObjectJ for the software package ImageJ (Abràmoff et al., 2004). We calculated relative head length and width values by two methods to account for body size. First, we used Mosimann's geometric mean (Mosimann, 1970) to correct for the effect of body size following Butler and Losos (2002). We calculated the geometric mean of all measured traits as the overall measure of size (SIZE), with the log-transformed version of the geometric mean size (log-SIZE) being the arithmetic mean of the log-transformed variables. Thus, log-SIZE for each individual was the mean of log(SVL), log(head length), and log(head width). The size-adjusted trait values for each individual were the log-transformed ratio of each trait to SIZE (log[trait/SIZE] = log[trait] − log[SIZE]). Second, we calculated residuals from linear regressions of log(trait) versus log(SVL) separately for each sex.

Population density and injury rates

Population density was calculated as the number of individuals per vegetated area of each island. We used vegetated area, rather than island size, to better represent the actual usable lizard habitat. We estimated population size with a log-linear capture–recapture method (Heckel and Roughgarden, 1979) based on a 3-day census on each island (see, e.g., Schoener et al., 2002, 2005; Pringle et al., 2007, 2015).

To assess whether intraspecific aggressive encounters increased with population density, we calculated the proportion of injured lizards on each island on the basis of X-ray images and scans. We compared injury percentages between males and females by Welch's t test to quantify sex differences in this proxy for aggressive encounters. We then used a linear regression model to test whether the percentage of injured lizards was related to population density. Percentages
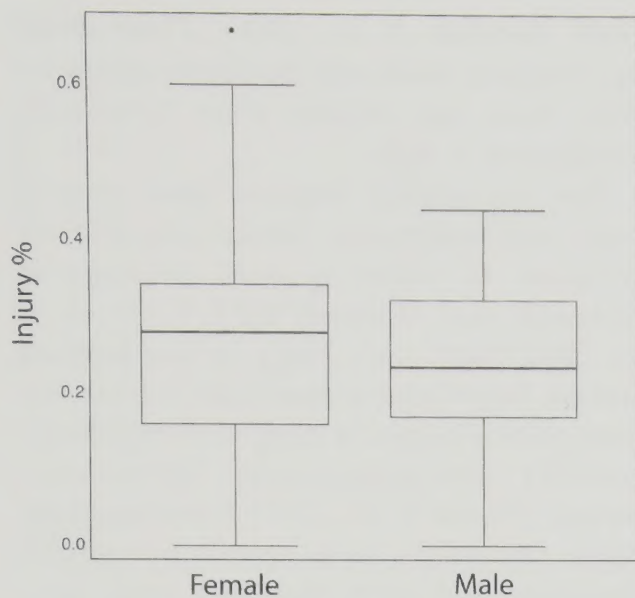
Figure 3. Box plots showing the overall injury percentages for male and female brown anoles from the 16 island populations.
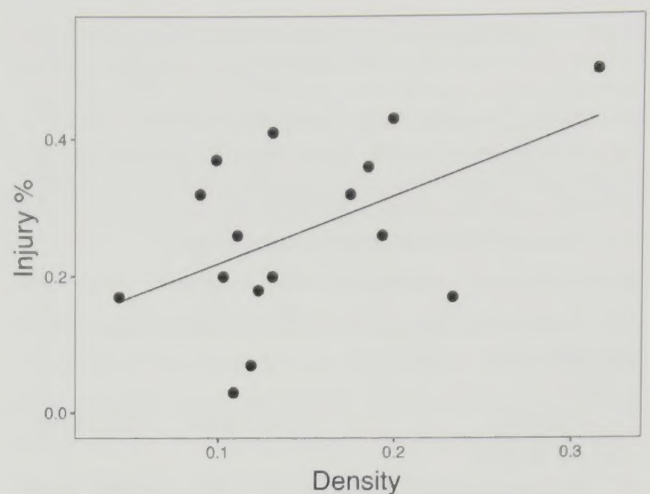

Figure 4. The percentage of injured lizards increased with population density across the 16 island populations of brown anoles. Injuries included missing claws, digits, and limbs; males and females are combined for each island.

were arc sine–transformed to improve normality before the analysis.

Morphologic variation and population density

We used linear regression analyses to test whether body size and head shape were related to population density. Log(SVL) was our measure of body size, and relative head length and width were calculated by both the geometric mean method and residuals, as described above. Because body size and relative head proportions are known to differ between male and female brown anoles, we conducted these analyses separately for each sex. All statistical analyses were conducted in R v3.3.2 (Pinheiro et al., 2016).

RESULTS

Percent injury for females was more variable among populations and marginally higher on average than for males (females = 29% $\pm$ 20%; males = 24% $\pm$ 12%), although this latter difference was not significant ($P = 0.62$; $t = 0.49$; df = 26.12;

Fig. 3). Therefore, we combined male and female injury rates in subsequent analyses. Injury rate showed a relatively weak but statistically significant positive relationship with population density ($P = 0.046$; $t = 2.18$; df = 14; $R^2 = 0.25$; Fig. 4), consistent with the hypothesis of greater intraspecific aggression at higher population densities.

We tested whether body size and head shape varied with population density in the direction predicted if stronger competition leads to selection on morphology. Body size and relative head width did not vary with population density for males or females (Table 2). In contrast, relative head length increased with population density for both sexes, and this relationship was stronger and more consistent for females than for males (Table 2; Fig. 5).

DISCUSSION

How morphologic traits of males and females relate to intraspecific competition is critical for advancing our understanding of evolution in polygynous mating systems (Kokko and Rankin, 2006). Using morpho-

TABLE 2. RESULTS OF LINEAR REGRESSION ANALYSES FOR THE RELATIONSHIP BETWEEN MORPHOLOGY AND POPULATION DENSITY USING MEANS FOR THE 16 ISLANDS FOR FEMALES AND MALES. BODY SIZE WAS LOG(SVL), AND RELATIVE HEAD LENGTH AND HEAD WIDTH WERE ADJUSTED FOR BODY SIZE BY BOTH THE GEOMETRIC MEAN METHOD [LOG(TRAIT/SIZE)] AND ANALYSIS OF RESIDUALS. STATISTICALLY SIGNIFICANT RELATIONSHIPS ARE IN BOLD.

	df	R^2	F	P
Females				
SVL				
log(SVL)	1, 14	0.04	0.62	0.45
Head length				
log(head length/SIZE)	**1, 14**	**0.51**	**14.50**	**0.002**
Residual head length	**1, 14**	**0.29**	**5.82**	**0.03**
Head width				
log(head width/SIZE)	1, 14	0.00	0.01	0.94
Residual head width	1, 14	0.02	0.23	0.64
Males				
SVL				
log(SVL)	1, 14	0.01	0.09	0.77
Head length				
log(head length/SIZE)	1, 14	0.11	1.81	0.20
Residual head length	**1, 14**	**0.28**	**5.43**	**0.04**
Head width				
log(head width/SIZE)	1, 14	0.00	0.04	0.84
Residual head width	1, 14	0.10	1.54	0.23

logic data from 16 island populations, we found evidence consistent with the hypothesis that intraspecific competition plays a role in shaping the morphology of male and female brown anoles. Lizards in high-density populations had a higher proportion of injuries compared with those in low-density populations, suggesting that the former experience higher levels of intraspecific aggression (Donihue et al., 2016). Lizards in these high-density populations had longer heads (when corrected for body size), a trait associated with dominance during intraspecific interactions (Gvozdík and Damme, 2003; Lailvaux et al., 2004; Perry et al., 2004). Relative head length increased for both males and females, and injuries were similarly frequent in both sexes, which suggests that females may participate in agonistic intraspecific interactions (Calsbeek and Smith, 2007; Calsbeek,

2009; Donihue et al., 2016). Thus, dominance-related traits may be advantageous for both males and females when intraspecific competition is high.

The relationship between head proportions and dominance during agonistic encounters in males is well documented (Gvozdík and Damme, 2003; Lailvaux et al., 2004; Perry et al., 2004). In several lizard species, larger head proportions increase bite force, which in turn is associated with larger territory sizes and greater reproductive success (Herrel et al., 2010; Donihue et al., 2016). Our results are in agreement with this prediction and show that both sexes have larger heads (specifically, longer heads relative to body size) in populations with higher densities. In males, selection might drive head shape variation because of the beneficial effect of bite force, similar to patterns observed in other lizard species (Herrel et al., 2010; Donihue et al., 2016). Whether selection acts in a similar manner on head shape in females is not known, but future studies that assess whether head shape in females increases social dominance and reproductive success would be informative.

In agreement with previous studies, our findings suggest that the frequency of aggressive encounters leading to injuries increases with population density (Vervust et al., 2009; Donihue et al., 2016). However, because populations with higher densities have larger heads, and head size typically increases bite force (Herrel et al., 2001, 2007, 2010; Verwaijen et al., 2002; Wittorski et al., 2016), we acknowledge that injuries might be more frequent in high-density populations owing to greater bite force, rather than more frequent aggressive encounters. Future work could combine injury data with behavioral observations to evaluate these possibilities.

The overall proportion of injuries in our study did not differ between males and females, suggesting that both sexes engage
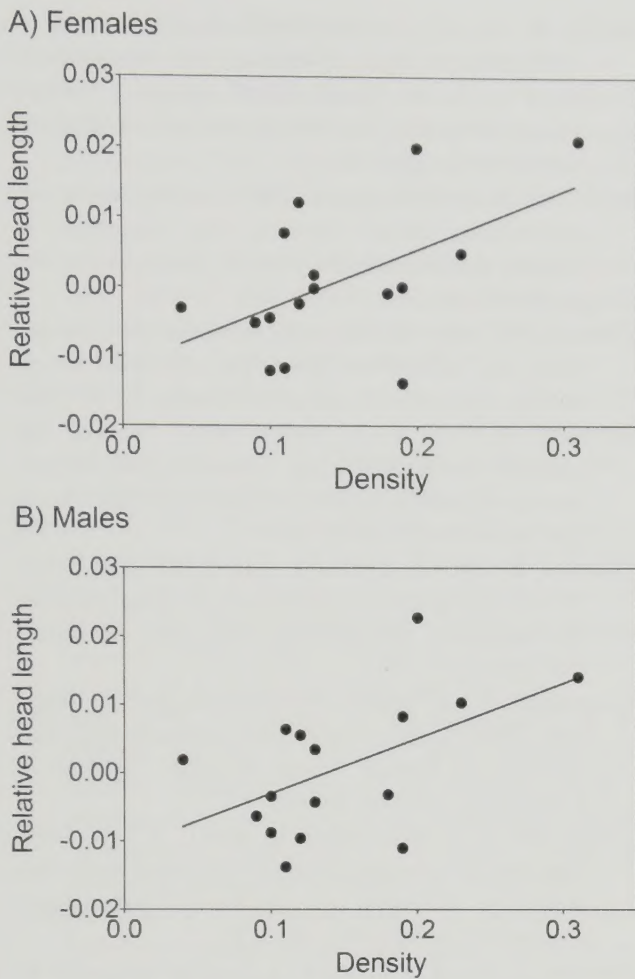
A) Females

B) Males

Figure 5. Relative head length increased with population density for both (A) female and (B) male brown anoles across the 16 island populations.

in aggressive behavior. Our findings are inconsistent with the assumption that males engage substantially more in aggressive behaviors than females in polygynous mating systems (Kokko and Rankin, 2006). Indeed, empirical studies have not established any consistent relationship between sex and injury, with some studies finding no difference between the sexes (Vervust et al., 2009; Donihue et al., 2016), and others finding a higher proportion of injuries in males (Gvozdik, 2000) or in females (Passos et al., 2013). The extent to which sexes differ in aggressive behavior needs to be determined in future studies by including behavioral observations of natural populations or

behavioral experiments that include both males and females.

Other ecological and evolutionary factors can influence both head size and injury rate, but we do not believe that these factors provide compelling alternative explanations for our results. For example, variation in head size could be related to differences in the prey species present on different islands, but this would not in itself explain the positive correlation between head length and population density. Moreover, dietary analysis of these same populations in 2013–2014 found that the most frequently consumed prey species (e.g., the cockroach *Hemiblabera pabulator* and the beetle *Artipus floridanus*) were present on all islands (Kartzinel and Pringle, 2015; Pringle et al., 2019). Predators can also influence morphology and cause injuries, but brown anoles were the top predators on these islands in 2011, aside from transiently present birds (Pringle et al., 2019). And whereas previous studies indicate that predation by birds tends to be greater on larger islands (Schoener et al., 2005), lizard density was not significantly related to island size in our data, suggesting that avian predation cannot explain the observed correlations between morphology and population density. Finally, it is possible that patterns in female head size are influenced by selection on male head size if they share a common genetic basis in the same populations. We do not believe that this is a parsimonious interpretation of our results, although further work is required to rule it out.

CONCLUSION

Our findings suggest that the current understanding of polygynous mating systems in *Anolis* lizards is incomplete with respect to females and their role in intraspecific competition. Sexual dimorphism and head shape variation have been attributed to sexual

selection enhancing male performance during agonistic encounters (Lailvaux et al., 2004; Perry et al., 2004; Jenssen et al., 2005; Donihue et al., 2016). This conclusion is based mainly on the assumption that females engage substantially less in aggressive and territorial behavior. Our results show that relative head size, a trait related to dominance, increased in both males and females with increasing population density. Injuries were detected in both sexes and were related to population density, suggesting that females engage in aggressive intraspecific encounters as well. Previous associations of head size and bite force indicate that both males and females might benefit from enhanced performance when levels of competition are high (Calsbeek and Smith, 2007; Calsbeek, 2009; Herrel et al., 2010; Donihue et al., 2016). Thus, females may play a more active role in agonistic intraspecific competition than previously assumed. Additional data are needed to examine whether female aggressive encounters are restricted to intrasexual interactions or involve both sexes, and whether female dominance increases reproductive success similar to the pattern observed in males.

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